

## LIFE-HISTORY PATTERNS AMONG CARABID SPECIES

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Evolutionary biologists aim to get a grip on evolutionary processes by assuming that natural selection would control special life-history traits, which are assumed to promote the fitness of species. With the help of models they try to explain the effect of special life-history traits in the evolution of life histories in general. Many of the models used are, in fact, extensions of the concept of *r* and *K* selection or are based on similar deterministic ideas. Examples of vertebrates are usually preferred, though invertebrates are thought to be subject to the same 'rules'. In the present paper by comparing the more generally occurring life-history traits among carabid species it is tried to find out which life-history traits dominate the life histories of West-European carabid species. Most of these traits governing the populations of carabid species of Drenthe (the Netherlands) appear to differ from those advanced by evolutionary biologists. 'Dispersal power' and 'turnover frequency' are especially significant. They show remarkable departures from the generally accepted schemes. These divergencies are explained and the possible causes of diverging life-history traits among carabid species are discussed. The need to do more comparative investigations of life-history traits in groups of related species in order to test the current thoughts about the role of life-history patterns in the course of evolution is emphasized.

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Since the publication of MacArthur & Wilson's 'Island biogeography' (1967), in which the concept of *r* and *K* selection was introduced, the study of life-history traits has become highly fashionable, especially among population ecologists and American evolutionary biologists. It is a pity, however, that these studies were mainly restricted to vertebrates and were theoretical. Apparently, many evolutionary biologists thought it possible to predict which life-history patterns (combinations of life-history traits) were most important for evolutionary progress, and with the help of mathematical models they tried to illustrate the effects of these life-history patterns on the success and survival of species (e.g. Gadgil & Bossert 1970, Cody 1971, Schaffer 1972, 1974a, b).

This trend in evolutionary biology was severely criticized by Stearns (1976). Regrettably, however, Stearns did not suggest doing comparative investigations among genetically related species on life-history traits in relation to the prevailing properties of the environments where these respective species thrive best (are most 'fit'). It might be expected that life-history traits, which improve survival and reproduction, are most favoured by natural selection in environments where the species is most fit. Therefore, when com-

paring these life-history traits for genetically related species, i.e. species in the same taxonomic group (see e.g. Den Boer 1980), but living in different kinds of habitat, one can expect to get some insight into the relationship between life-history patterns and prevailing environmental conditions. It would especially be interesting, to check whether or not the theoretically predicted patterns indeed emerge as the most important patterns from such a comparative field study.

After a symposium 'On the evolution of behaviour in carabid beetles' (Den Boer et al. 1979), and stimulated by the paper of Stearns (1976), the first author tried to make a provisional comparison of the life-history traits of carabid species of stable habitats (forests) with those of carabid species of unstable habitats (banks of rivers and pools, and agricultural fields) (Den Boer 1979a). Since that time the comparison of life-history traits always has been a point of general interest somewhere in the background of the investigations on the population dynamics of carabid beetles at the Wijster Biological Station.

In the present paper we will give and discuss the results of a comparison of life-history patterns among the carabid species of our area (Drenthe), which are representative for the greater part of western Europe.

Therefore, we will first discuss the concept of *r* and *K* selection of MacArthur & Wilson (1967), then the life-history traits considered to be most important by Stearns (1976), and finally we will compare these with our present knowledge of life-history patterns among carabid species.

#### *r* and *K* selection

The best known and most cited attempt to connect animal numbers with life-history patterns was the introduction of the dichotomy of species into *r*-selected and *K*-selected species by MacArthur & Wilson (1967). This dichotomy was based upon the well-known equation for logistic population growth of Verhulst (1838):  $dN/dt = rN(K-N)/K$ , in which *r* is the 'intrinsic rate of natural increase', i.e. the maximum potential rate of reproduction, and *K* is the carrying capacity of the environment, i.e. the maximum number of individuals the habitat can support under the current conditions.

'As an example of how *K* selection and *r* selection can be in opposition, consider different situations in which crowding can either reduce the per capita food supply to a precariously low level, or else not have this effect. In an environment with no crowding (*r* selection), genotypes which harvest the most food (even if wastefully) will rear the largest families and be most fit. Evolution here favors productivity. At the other extreme, in a crowded area (*K* selection), genotypes which can at least replace themselves with a small family at the lowest food level will win, the food density being lowered so that large families cannot be fed. Evolution here favors efficiency of conversion of food into offspring – there must be no waste' (MacArthur & Wilson 1967: 149).

Note that the concept of *r* and *K* selection is entirely theoretical. It is based on a very simple and unidirectional notion of natural selection. Den Boer et al. (1993: 257/258) wrote about natural selection: '... the longer a natural population persists in a certain area, the better will the frequency distribution of genotypes fit the distribution of selective events, which is the same as saying, the better the population becomes adapted to the variability of local conditions. ... In our opinion this state of affairs is the base for significant evolutionary processes, because such processes can only continue over a sufficiently long period as long as natural selection can shift from one genotype to another within a very broad frequency distribution of genotypes, i.e. a frequency distribution that has developed and was moulded under environmental conditions that varied in space and time and was maintained by risk spreading.'

Nevertheless, the concept of *r* and *K* selection got much attention among population ecologists, who often called the species they studied either *r*- selected

or *K*-selected, without, in most cases, doing any research into the suggested selection processes. Meanwhile, the usage of these terms has so broadened that almost any life-history dichotomy is likely to be termed *r* and *K* selection (Atkinson 1979). Parry (1981) recognized four different meanings for the terms *r* and *K* selection:

a) *r* selection is selection for maximum population growth in uncrowded populations; *K* selection is selection for competitive ability in crowded populations. This is the original meaning, which we cite above.

b) *r* selection is the density-independent component of natural selection; *K* selection is the density-dependent component of natural selection. (This density-dependent component can be crowding, but it might also be predation, or parasitism, etcetera).

c) *r* species occur in habitats which are ephemeral; *K* species occur in habitats with a long durational stability. (Apart from the fact that stability of a habitat will directly affect many life-history traits and thus natural selection, mainly in a stable habitat the available time for population growth can be expected to be sufficient to result in crowding).

d) *r* selection is the allocation of a large proportion of resources to reproduction; *K* selection is the allocation of a small proportion of resources to reproduction. (High reproductive effort should be associated with small young, and low reproductive effort with large young).

For a review of the publications in which these different meanings of *r* and *K* selection are used we refer to Parry (1981). Although the concept of *r* and *K* selection has stimulated much of the recent research into life-history patterns, it has also led to considerable confusion around life-history traits and population numbers.

It will be evident that knowledge about the relationship between life-history patterns and population numbers cannot only be based upon theoretical concepts that in the field usually are difficult to quantify reliably; for example, the amount and direction of selection processes, the numerical effect of density-dependent versus density-independent mortality, the degree of stability of habitats, or the allocation of resources to reproduction or otherwise. The inclusion of such appealing but vague concepts will mostly only contribute to vaguely formulated investigations and ambiguous results.

Therefore, it seems preferably first to find out what are the most important life-history traits, and the most frequently occurring life-history patterns in field populations, and then theorize about the possible significance of these patterns for the course of evolution, and not the other way round. See also Stearns (1992: 206/207).

### The life-history traits recognized by Stearns (1976)

In an extensive and critical review of the literature Stearns (1976) tried to summarize our present knowledge about the relationship between life-history traits and principal features of the environment. He especially criticized the fact that conclusions are drawn from models that were not tested in the field: 'First, theories accumulate, few of them formulated in common terms, much faster than evidence can be assembled to test them. The result is confusion of untested ideas which are judged, not on their ability to withstand empirical tests, but on the difficulty of the mathematics used or the obscurity of the theoretical development' (l.c.: 36). It can be added that the mod-

els developed, in some way or another, are extensions of the logistic growth equation and thus of the ideas of  $r$  and  $K$  selection of MacArthur and Wilson.

Other of Stearns' criticisms concern the patterns of causation: 'Within the biological community, there is a subterranean split between those who believe that for every phenomenon there is a single cause at a given level of explanation, and those who believe that there can be multiple causes for certain phenomena operating at the same level of explanation' (l.c.: 37). The idea of multiple causes is worked out and illustrated with enlightening examples in Hilborn & Stearns (1982). In his paper of 1976 Stearns tried to find out which combinations of life-history traits

Table 1. Number of eggs laid in three succeeding years by each of 30 females of the carabid beetle *Pterostichus versicolor* (= *coeruleescens*) in the laboratory at 19 °C and with superabundant food. All females reproduced for the first time in 1976; hibernation occurred in the field (modified after Van Dijk 1982: table 5).

	Number of eggs laid in			total number of eggs laid
	1976	1977	1978	
1	0	92	0 +	92
2	0 +	—	—	—
3	1	3	224	228
4	1	98	59 +	158
5	3	72 +	—	72 *
6	5	61	164	230
7	9	2	94	105
8	11	5	87	103
9	25	18	31 +	74
10	42 +	—	—	42 *
11	45	89	171	305
12	48	276	291	615
13	72	50	169	291
14	79	1 +	—	80 *
15	79	10	204	293
16	81	88	278	447
17	83	169 +	—	252 *
18	93	215 +	—	308 *
19	93	32	292	417
20	95 +	—	—	95 *
21	112	87	0 +	199
22	115	17	89	221
23	119	280	146	545
24	122	114	114	350
25	124	95 +	—	219 *
26	128	54	70 +	252
27	134	252	0	386
28	147 +	—	—	147 *
29	197 +	—	—	197 *
30	261	315	98	674
Total	2324	2495	2581	5984 +
mean	77.5 ± S.E. 11.94	99.8 ± S.E. 19.26	129.1 ± S.E. 21.04	1412 *
N	30	25	20	

+ = died during hibernation in the field; \* = total number of eggs laid by females that did not complete all three reproduction periods.

After reproduction had finished the individually brand-marked females were placed in large enclosures in the field to hibernate; as far as not died in winter the females were recaptured in early spring by placing many small pitfalls along the inner sides of the enclosures.

have evolved most frequently to counter specific difficulties for survival and reproduction offered by the environment, i.e. which traits most directly determine the 'fitness' of the species.

He calls such combinations of life-history traits 'tactics': 'I define a tactic as a set of coadapted traits designed, by natural selection, to solve particular ecological problems' (Stearns 1976: 4). We prefer it to call such combinations of traits 'life-history patterns', in order to avoid any suggestion of teleology.

The life-history traits that should affect fitness most according to the current literature (Stearns included) are: (1) brood size; (2) relative size of the young; (3) the age distribution of reproductive effort, i.e. semelparity (a single reproduction period per female), and iteroparity (repeated reproduction by each female); (4) the interaction of reproductive effort with adult mortality, i.e. the possible occurrence of a 'trade-off' between fecundity and survival of adults; (5) age at first reproduction.

#### Life-history traits in fluctuating environments

In seasonal environments with an unpredictable start of the favourable season Stearns expected that '... the optimal tactic consists of generating a distribution of hatching times in the clutch that matches the historical probability distribution of the optimal date for reproduction' (l.c.: 28). He based this expectation on the 'spreading of risk' hypothesis of Den Boer (1968).

Environmental conditions that vary from year to year would select clutch sizes both smaller and more variable than the most productive size. In this connection Stearns refers to a paper by Murdoch (1966), in which he stated that carabid beetles live longer and survive into the next season after having decreased their reproductive effort, i.e. a trade-off between survival and fecundity.

This conclusion of Murdoch (1966) was severely attacked by Van Dijk (1979), who especially blamed Murdoch for not having studied the fecundity of surviving beetles in following seasons. Table 1 clearly shows that after the first reproductive season the total reproductive effort (number of eggs laid) of surviving beetles ( $n= 25$ ) and of beetles that did not survive the first winter ( $n= 5$ ) did not differ significantly (Mann-Whitney:  $P= 0.28$ ). The same applies to the second reproductive season, both for the numbers of eggs laid during two seasons ( $n= 20$  and  $n= 5$ ;  $P= 0.46$ ), and for those laid during the first season only ( $P= 0.38$ ). But the beetles that survived all three reproductive seasons did produce significantly more eggs during these three seasons than those that died during the third winter ( $P= 0.0073$ ), i.e. just the reverse of what would be expected from a trade-off between reproduction and survival. Both during the first season and during the first two seasons the beetles that sur-

vived all three seasons did not produce numbers of eggs that were significantly different from those of beetles that died during the last winter ( $P= 0.20$  and  $P= 0.36$  respectively). See also Van Dijk (1994), where it is shown that similar results are obtained when the beetles are not fed 'optimally' as occurred in the experiments of Van Dijk (1979). The greater reproductive capacity of the beetles that survived all three winters became apparent only during the third reproductive season.

Of course, this does not mean that in other species a trade-off between reproduction and survival may not occur. But we have the impression that, on theoretical arguments alone, it is too often assumed that such a trade-off would occur, whereas it is only rarely demonstrated in reliable field data or tested by experiments (see also Stearns 1992: Appendix 2).

This is not a biased statement, but is based on careful studies. Aukema (1990a) studied the genetics of the wing-dimorphism in three species of the carabid genus *Calathus*. Among other things he wanted to know whether or not there are other differences between the long-winged and short-winged morphs than the difference in wing development. Contrary to our expectations, he found that the long-winged morph produced significantly more eggs over a longer period than the short-winged morph (Aukema 1991, 1994).

Hence, the extra reserves used by long-winged beetles to produce large wings and wing-muscles did not frustrate the production of eggs as compared with egg production of short-winged beetles, i.e. there was no 'trade-off' between the forming of large wings and wing-muscles and the size of egg production, on the contrary. In retrospect the above results are not unreasonable, because the long-winged beetles can fly away from the population and colonize vacant sites. And colonization has a better chance of success when the beetles produce as many eggs as possible. But this story also illustrates how careful one has to be when assuming a 'trade-off'.

Ideas about such trade-off's are based upon the 'budget-concept', i.e. each individual can dispose of similar and only restricted reserves, and these can either be used solely for high reproduction, or partly for other processes as well, such as the development of wings and wing-muscles, a longer life, etc., with lower reproduction as a consequence (e.g. Cody 1966). In our opinion, it is forgotten that individuals of the same species are not similar and can differ importantly in their basal metabolism (see e.g. Gotthard et al. 1994), which may lead to significant differences in development time, fecundity, longevity, etc. between individuals (compare Table 1).

As far as Stearns (1976) knew, no theoretical work had been done on optimal life-history patterns in en-

vironments that change randomly in time. He assumed that when conditions are favourable the optimal pattern should be: rapid development and a total commitment of available reserves to reproduction that produces a resting stage. Such a life history is indeed found among many animals and plants of deserts, e.g. in the brachiopod (Notostraca) *Triops cancriformis*, which develops rapidly and reproduces in temporary pools originating from heavy rainfall, followed by many years in a resting stage (eggs). A comparable situation is found in trees where the seeds are only released after a fire, which also creates the right conditions for germination of the seeds, e.g. in *Pinus contorta*.

'If progeny can grow faster as larvae outside the parent (when resources for the young are abundant and predation pressure is low), then many small progeny will be favored. If resources for young are scarce, or predator risk to small size classes is high, then the parent will tend to produce a few large progeny' (Stearns 1976: 31).

But Stearns realizes very well that there are many exceptions to this 'rule'. It is a pity that many evolutionary biologists immediately connect the production of many small young versus a few large ones to r and K selection, and thus omitted to observe the life history more closely. For instance, there are good reasons to assume that the production of big eggs, different kinds of parental care, the development of one or a few young inside the mother, etc. are not so much connected with an overall scarcity of resources for the young, but more with a high probability of the occurrence of unfavourable physical conditions for them. As well these traits may be associated with the difficulties of small young finding rapidly enough, sufficient of the most adequate – and possibly abundantly present – food to survive this early and most vulnerable stage of their development.

It is often stated that reproductive effort should increase with age. Indeed, Table 1 gives a clear example of that: in 10 out of 15 females that survived all three winters egg production was highest during the third reproductive season. And in three others of these females it was highest in the second reproductive season. Klomp (1970) found a similar phenomenon for the clutch sizes of birds, with the partridge from England as an exception. We expect, however, there will be more exceptions to this 'rule', and not only among birds. More of such 'rules' are constructed by evolutionary biologists (see e.g. Williams 1966), predominantly from theoretical considerations, such as optimization models. Hence the situation in evolutionary biology is similar to that in population ecology: too many theories, a predominance of deterministic or pseudodeterministic (see Feller 1939) models, insufficient reliable field observations, and a too de-

voted belief in simple 'rules'.

The new book of Stearns (1992) shows that the adequate study of life histories did not progress remarkably during the last decades, in spite of: 'Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles. Fascinating in themselves, life histories are also the keys to understanding related fields. Life history theory is needed to understand the action of natural selection, a central element of evolution, the only theory that makes sense of all of biology. It also helps to understand how the other central element, genetic variation, will be expressed. The evolution of life-history traits and their plasticities determines the population dynamics of interacting species. Its explanatory power, barely tapped, could reach as far as communities. There is much to be done' (l.c.: 9).

Broadly speaking, we agree with Stearns, especially with the very last sentence, and therefore it is the more regrettable that life-history theory is still largely based upon optimization models, trade-off's and deterministic mathematics. The book of Roff (1992) on the same subject gives a similar picture as that of Stearns about the study of life histories.

To generate testable hypotheses about the processes underlying life-history patterns it will be necessary first to do an extensive comparative investigation of life-history traits, their variation and combinations, among related species, and next to find out how the differences and variations of life-history traits among these related species might be connected with their genetics, dynamics, choice of habitat and food preferences. As advocated by Stearns (1976) only when sufficient investigations have been done might it be interesting to return to theoretical considerations and models: 'Not only do theories accumulate, but the manner of their accumulation decreases the likelihood that they will be tested. An enormous amount of effort is being put into the development of ideas for which no one has established connections with the real world. If the field is to progress, we must get away from the practically Scholastic approach surfacing in such papers, and get back to rigorous empiricism' (l.c.: 37).

## RESULTS

### Life-history patterns among carabid species

#### Carabid species from stable and from unstable habitats

Although we do not pretend to be able to improve life-history theory substantially – even less to tell evolutionary biologists how to do their research – we thought it useful to stimulate discussions about the

kind of results that might arise from a comparative study of life-history traits among related species. Den Boer (1979a: Tables 1 and 2) made a first step in this direction. He compared the life-history traits of the 14 most common carabid species of forests with those of the 16 most abundant carabid species of agricultural fields and waste sites, in order to approach the current interpretation of r and K selection as closely as possible (see Parry 1981).

In each of the groups there are both spring, summer, autumn and winter reproducing species (Den Boer et al. 1990). In both groups most species are iteroparous with only a single semelparous species in each group. We could not discover any striking difference in the numbers of eggs produced between species of the two groups, but this aspect asks for more painstaking investigations than have been done to date. More consistent differences in the life-history patterns between these two groups were found in a combination of night- or day-activity, degree of polyphagy, and powers of dispersal, especially presence or absence of dispersal by flight. Flight observations are made by catching flying carabid beetles with window traps (vertical glass plates, see Southwood 1976: 193). Such window traps were operating during more than 20 years around the Wijster Biological Station (Den Boer 1979a).

Taking together the results of this provisional study we got the impression that for carabid species of the temperate regions (at least in western Europe) among the more significant life-history traits dispersal power is most closely connected with the current environmental conditions. In other words, carabid species will show a rate of dispersal that is indicative of the rate of population 'turnover' (Den Boer 1977). Species living in rather stable habitats (forests, old heath areas, old peat moors) show a low population turnover and low powers of dispersal, because individuals leaving the population area usually have only a low chance of surviving and reproducing. Features favouring dispersal will be selected against. On the other hand, species living in ephemeral habitats (agricultural fields, banks of pools and rivers) are forced to show a high population turnover. Individuals leaving the population area may have a better chance to survive and reproduce than individuals staying there. In such species features favouring dispersal are not expected to be selected against (Den Boer 1990a).

Although evolutionary biologists usually do not consider 'dispersal power' to be a life-history trait, we neglect possible theoretical objections and, in the following, we will also call 'dispersal power' a life-history trait (see also Roff 1994). 'Dispersal power' determines the 'design for survival of the species' (Stearns 1976), since it might be connected with fecundity, as was shown by Aukema (1991, 1994) and was discussed before.

In 1992 Stearns (p.10) says: 'Life history traits figure directly in reproduction and survival.' Indeed, dispersal power does usually figure in reproduction and survival, but indirectly, i.e. by opening the possibility to found new populations. In this case it would not be a direct 'fitness-feature', but an indirect one.

#### Comparison of life-history traits of carabid species with theoretical expectations

About some life-history traits that are highly valued by evolutionary biologists we can establish the following for carabid beetles:

a) 'Concerning relative size of the young'. All carabid species, just like many other insects (Ross 1956: 165), lay relatively big eggs with much yolk, which will give the young larvae a reasonably good start after hatching. But there are differences: *Carabus*-species (adults 14-26 mm) especially develop and lay relatively low numbers of rather big eggs, as do some small carabids, such as some species of *Trechus* and *Bembidion* (adults 2-5 mm). On the other hand, some *Calathus*-species (adults 8-14 mm, Aukema 1991), and *Nebria brevicollis* (10-12 mm, Nelemans 1987) lay many much smaller eggs. Within the same population of a species eggs usually are of the same size (but see Ernsting & Isaaks 1994).

Many carabid beetles exhibit some kind of simple parental care, especially *Abax*-species (Brandmayr et al. 1979) and some other species of forests. As far as there is some relationship with environmental conditions, we can establish that most *Carabus*- and all *Abax*-species occupy forest areas. There are no indications, however, that parental care would have anything to do with competition, i.e. with K selection.

b) Most carabid species are iteroparous (more than one reproduction period per female). The few semelparous species known so far are not especially living under conditions of r-selection: *Nebria brevicollis* prefers light forest, though it also occurs in other more or less shaded sites; *Loricera pilicornis* occupies wet shaded sites (Lindroth 1945: 1992). Population numbers of semelparous species fluctuate more widely than those of iteroparous species living under similar conditions. An example of such a difference in field populations is given by Den Boer (1979b: 163, and fig. 3). The semelparous species mentioned by Den Boer (1979a) are more or less specialized for the catching of collemboles (Hengeveld 1980).

c) The interaction of reproductive effort with adult mortality (trade-off) for carabid beetles was discussed before.

d) Concerning 'age at first reproduction' we can confirm that most autumn breeding carabid species reproduce immediately after eclosion of the adults (e.g. *Calathus melanocephalus*. Van Dijk 1972, 1973). But the advantage of a low chance of dying at this

time is more than nullified by the long larval development of 7-9 months in the most unfavourable season (winter) when mortalities are very high (Van Dijk & Den Boer 1992: tables 4, 5, 6).

Young beetles of the semelparous autumn breeder *Nebria brevicollis* aestivate for 2-3 months before reproducing in September-November, and this is accompanied by an additional mortality of 10-30% (Nelemans et al. 1989). This apparently unfavourable way of life is undoubtedly connected with the origin of *Nebria*-species as inhabitants of cold regions, such as northern Canada, northern Scandinavia and higher regions of the Rocky Mountains and the Alps, where the young beetles have to overwinter before reproducing (Kavanaugh 1985; Gereben 1994). Hence, *N. brevicollis* is 'locked in', so to speak, to a way of life that was adequate for its ancestors. It may no longer be able to 'escape' from that, in spite of the disadvantages connected with a life-history pattern that combines semelparity, autumn breeding and aestivation. Although this life-history pattern is far from 'optimal' (see also: White 1993), *N. brevicollis* is an abundant species in temperate Europe and it thrives well there, albeit with wide fluctuations of numbers (Den Boer 1979b: fig. 3).

Spring breeding carabid species have the advantage of a short larval development, though often under too dry conditions, but young beetles have to overwinter before reproducing, which is accompanied with appreciable mortality (Den Boer 1979b: table 2). Possibly, some winter breeders have combined larval development in spring and summer with reproduction of just eclosed beetles in winter and early spring. But in many winters weather conditions are such that any kind of activity, let alone reproduction, is impossible. So, per force and at the cost of high losses, winter breeders become early spring reproducers. Moreover, some winter reproducers, e.g. *Bradyceillus harpalinus*, migrate before reproduction. This, too, introduces high mortalities.

Among carabid species there is no distinct relationship between 'time of reproduction' and environmental conditions, with the trivial exception that in open, wet sites only spring breeders occur, simply because larvae cannot survive in sites that are usually inundated in winter and early spring. Also, in dry heathland and blown sand areas with sparse vegetation, mainly winter breeders occur, possibly because the very small first instar larvae of these species can only escape desiccation in these dry habitats in winter and early spring. But in other kinds of habitat in the Netherlands carabid species reproduce in many different times of the year: Den Boer (1980: table 3; Den Boer et al. 1990). See also Greenslade (1965) and Murdoch (1967).

### A general comparison of life-history patterns of carabid species living in Drenthe (The Netherlands)

The comparison of carabid species from forests with those from unstable habitats may be biased in that it might give a too clear dichotomy. It is not sure, of course, that species from other kinds of habitat will nicely fit into the picture developed above. Therefore, it is advisable also to make a more general comparison of the life-history traits of carabid species. For methods of the collection of necessary data we refer to Den Boer (1977), with the remark that the data used in the following do not cover the period 1959-1967 as in Den Boer (1977), but the period 1959-1985.

Figure 1, in which 68 carabid species are ranked according to the period of reproduction, distinctly illustrates that in each time of the year reproduction is possible for at least some carabid species. The period of reproduction is not related to dispersal power: relatively good dispersing species (m and d) as well as poorer dispersing ones [(m), (d) and b] are distributed randomly among the 68 species (Mann-Whitney:  $P=0.77$ ). In relatively stable habitats (F, H, S, H+S, H+P, H+F, F+R) significantly more carabid species are autumn breeders (asterisk in fig. 1) than in less stable habitats (W, A, R, W+A, A+R, S+A, S+R, H+W): Mann-Whitney,  $P=0.0003$ . Autumn breeding seems to be a life-history trait that is closely connected with stability of the habitat.

Well dispersing carabid species, which are not only fully winged or wing-dimorphic with a high fraction of winged specimens, and are also observed in active flight (catches in window traps), are more often found in less stable habitats than carabid species with low powers of dispersal, i.e. no flight observations and often unwinged or wing-dimorphic with a low fraction of winged specimens:  $r_s$  (Spearman) = +0.42 ( $P=0.0006$ ). As discussed by Den Boer (1990a) carabid species living for many generations in stable habitats gradually lose 'dispersal power' (reduction of both wing-muscles and hindwings). This process again diminishes the number of opportunities to found new populations by flying individuals, in which genes associated with dispersal might be multiplied.

This process towards brachyptery in stable habitats has been advanced by the changing of stable habitats into less stable agricultural fields by man, causing the remnants of stable habitat to become highly fragmented and isolated. As a result brachyptery is most likely to be strongly associated with stability of the habitat in forests, usually the oldest remnants of stable habitat in cultivated regions, more so than in heath areas. In our area, however, old forest has nearly completely disappeared, while stable heath areas are highly fragmented and at most a few thousands years old.

species	no.	habitat	dp	Mar	Apr	May	June	July	August	Sept	Oct	Nov	Dec	Jan	Feb															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>Asaphidion flavipes</i>	44	H+A	m	oooooooooooo																										
<i>Pterostichus nigrita/rhaeticus</i>	137	W	m	oooooooooooo																										
<i>Pterostichus diligens</i>	133	W	d	oooooooooooooooo																										
<i>Pterostichus minor</i>	135	W	d	oooooooooooo																										
<i>Pterostichus strenuus</i>	139	F+W	(m)	oooooooooooo																										
<i>Pterostichus oblongopunctatus</i>	138	F	(m)	oooooooooooo																										
<i>Pterostichus quadrifoveolatus</i>	130	B	m	oooooooooooo																										
<i>Syntomus foveatus</i>	114	H+S	(d)	oooooooooooo																										
<i>Agonum assimile</i>	6	F	(m)	oooooooooooo																										
<i>Agonum ericeti</i>	8	H+P	b	ooooooo																										
<i>Amara communis</i>	26	A+R	m	oooooooooooo																										
<i>Amara familiaris</i>	31	A+R	m	oooooooooooo																										
<i>Carabus nemoralis</i>	78	F	b	oooooooooooo																										
<i>Loricera pilicornis</i>	112	W	m	oooooooooooooooo																										
<i>Pterostichus versicolor</i>	132	H	(m)	oooooooooooooooo																										
<i>Notiophilus aquaticus</i>	119	H	(d)	oooooooooooooooooooo																										
<i>Notiophilus palustris</i>	122	F	d	oooooooooooo																										
<i>Notiophilus rufipes</i>	124	F	(m)	oooooooooooo																										
<i>Agonum sexpunctatum</i>	18	W	m	oooooooooooo																										
<i>Clytina fuscior</i>	86	H+A	d	oooooooooooo																										
<i>Harpalus affinis</i> X	99	A	m	oooooooooooo																										
<i>Harpalus latus</i> *	103	H+F	(m)	oooooooooooo																										
<i>Notiophilus biguttatus</i> X	120	F	d	oooooooooooo																										
<i>Carabus cancellatus</i> X	76	H	b	oooooooooooo																										
<i>Calathus rotundicollis</i> *	73	F	d	oooooooooooo																										
<i>Cymindis macularia</i> *	88	S	b	oooooooooooooooo																										
<i>Bembidion lampros</i> X	54	W+A	d	oooooooooooo																										
<i>Harpalus quadripunctatus</i> *	105	F	m	oooooooooooo																										
<i>Abax parallelepipedus</i> *	1	f	b	oooooooooooo																										
<i>Agonum fuliginosum</i> X	9	F	d	oooooooooooo																										
<i>Anisodactylus binotatus</i> X	42	A	m	ooooooo																										
<i>Harpalus solitarius</i> *	102	H	m	ooooooo																										
<i>Agonum obscurum</i> *	17	H	(d)	oooooooooooo																										
<i>Pterostichus lepidus</i> X	134	H+S	b	oooooooooooo																										
<i>Harpalus rufipes</i> *	104	A	m	oooooooooooo																										
<i>Amara plebeja</i> X	35	A	m	oooooooooooo																										
<i>Amara lunicollis</i> X	34	H+W	m	oooooooooooo																										
<i>Harpalus rufipalpis</i> *	106	R	m	oooooooooooo																										
<i>Pterostichus melanarius</i> *	141	A	(d)	oooooooooooo																										
<i>Trechus secalis</i> *	148	F	b	oooooooooooo																										
<i>Cymindis vaporariorum</i> *	89	H	d	oooooooooooo																										
<i>Leistus terminatus</i> *	109	F+H	(m)	oooooooooooo																										
<i>Calathus erratus</i> *	68	H+S	(d)	oooooooooooo																										
<i>Broscus cephalotes</i> *	66	S	m	oooooooooooo																										
<i>Amara brunnea</i> *	25	F	m	oooooooooooo																										
<i>Calathus melanocephalus</i> *	70	H	(d)	oooooooooooo																										
<i>Amara equestris</i> *	29	H	(m)	oooooooooooo																										
<i>Pterostichus niger</i> *	136	F+R	(m)	oooooooooooo																										
<i>Trechus obtusus</i> *	146	F+R	d	oooooooooooo																										
<i>Notiophilus germinyi</i> *	121	S	d	oooooooooooo																										
<i>Olisthopus rotundatus</i> *	125	H	(d)	oooooooooooo																										
<i>Calathus fuscipes</i> *	69	S+R	d	oooooooooooo																										
<i>Carabus problematicus</i> *	80	F	b	oooooooooooo																										
<i>Nebria brevicollis</i> *	117	F	m	oooooooooooo																										
<i>Nebria salina</i> *	118	H	m	oooooooooooo																										
<i>Leistus rufomarginatus</i> *	110	F	(m)	oooooooooooo																										
<i>Trichocellus placidus</i> X	150	F	m	oooooooooooo																										
<i>Trichocellus cognatus</i> X	149	H	m	ooooooo																										
<i>Bradyccylus ruficollis</i> X	65	H	m	oooooooooooo																										
<i>Bradyccylus harpalinus</i> *	64	H	d	oooooooooooo																										
<i>Amara infima</i> X	33	S	(d)	oooooooooooo																										
<i>Bembidion nigricorne</i> X	56	S	b	oooooooooooo																										
<i>Bradyccylus caucasicus</i> X	62	H	d	oooooooooooo																										

Nevertheless, both in remnants of forest and in those of heath we find about the same numbers of species with low powers of dispersal [(m),(d) and b] and with high powers of dispersal (m and d) respectively:  $\chi^2 = 0.138$  (d.f.=1,  $P=0.70$ ), this most probably because remnants of really old forest in the Netherlands have either disappeared completely or are too small to keep viable populations of poorly dispersing carabid beetles for a long time. However, among the four macropterous forest species only *Trichocellus placidus* (150), a species of small patches of young forest and of forest borders, is regularly caught in window traps (in flight), whereas among the six macropterous species of heath there are three regular flyers, *Amara lunicollis* (34), *Trichocellus cognatus* (149) and *Bradyceillus ruficollis* (65).

So far the general conclusions drawn from fig. 1 do not deviate significantly from those reached by Den Boer (1979a), who compared 14 forest species with 16 species from unstable habitats.

The picture can be completed now with: (a) Spring breeders can be found both in stable and in unstable habitats, autumn breeders mainly in stable habitats, but winter breeders are almost restricted to sandy sites. (b) The still surviving poorly dispersing species are mostly found in remnants of stable habitat, whereas well dispersing species occur both in stable and in unstable habitats with some preference for the latter.

Grüüm (1984) suggested that the fecundity of autumn breeders would be higher than that of spring breeders. In general we have the same impression (Nelemans 1987; Aukema 1991; Van Dijk & Den Boer 1992), though we wonder whether the autumn breeder *Carabus problematicus* will fit this picture (Rijnsdorp 1980): females of *C. problematicus* produce low numbers of rather big eggs, whereas females of the autumn breeding *Calathus*-species and of *Nebria brevicollis* produce many rather small eggs. The actual egg production has to be studied more closely, since data from the dissection of females often are not reliable (Van Dijk 1986b).

### Life-history patterns among closely related species

Figure 1 enables us to study the effect of genetic relationships on life-history traits, assuming that taxonomically related species are also genetically related (compare Den Boer 1980). When comparing species within genera we find that some genera are rather homogeneous, i.e. characterized by a special life-history pattern:

*Calathus*-species are wing-dimorphic (except *C. mollis*), night-active, autumn breeding, polyphagous carnivores, which lay many small eggs. Most *Harpalus*-species (in fig. 1: 5 out of 6) are macropterous, polyphagous autumn breeders that also consume plant material and mainly occupy poor grassy sites (Desender & Turin 1989; Turin et al. 1991); *Bradyceillus*-species are polyphagous, macropterous or wing-dimorphic winter breeders of sandy sites; *Agonum*-species and most *Amara*-species (in fig. 1: 6 out of 9) are spring or early-summer breeders. Most *Amara*-species are polyphagous (including plant material) and macropterous (in fig. 1: 7 out of 9) species of unstable habitats, whereas the four *Carabus*-species in fig. 1 are brachypterous, lay a few relatively big eggs, and are associated with stable habitats; they are polyphagous carnivores that digest their prey outside the body by bringing digesting fluids into it. *Nothiophilus*-species are all very similar looking (fast running, small beetles with large eyes), oligophagous hunters of collemboles (Hengeveld 1980), which often show diverging reproduction periods (119: *aquaticus*, 120: *biguttatus*); *Leistus*-species are night-active, oligophagous hunters of springtails with specialized morphological adaptations for catching their rapid prey, and which reproduce late in autumn after a period of aestivation; in many respects *Nebria*-species resemble *Leistus*-species, except for the morphological adaptations to catch springtails.

But other genera, for instance *Pterostichus*, are very heterogeneous in many respects: dispersal power is very different among the 11 species of fig. 1 (3 m, 3 d, 3 (m), 1 (d), 1 b), 8 species are spring breeders, one

Fig. 1. Reproductive periods of the 68 most abundant carabid species of Drenthe (the Netherlands) ranked from early reproducers (March-May) until late reproducers (October and in winter, sometimes continued in early spring). For each species the expected dispersal power (dp) is indicated: m= fully winged (macropterous), (m)= wings relatively small, often not suitable for flight, d= wing-dimorphic with a high fraction of fully winged specimens (>2%), (d)= wing-dimorphic with a low fraction of fully winged specimens (< 2%). Also the preferred habitat of each species is indicated: W= wet, open habitats, e.g. banks of pools and small rivers, B= sites where forest or peat has been burned, R= ruderal and other waste sites, A= agricultural fields, S= blown sand areas fixed by vegetation and dry heathland, H= mainly moist heathland, P= peat moor, F= forest. Species indicated by an asterisk must be considered autumn breeders with winter larvae, those indicated by an X possibly also are autumn breeders, but the presence of winter larvae is not convincingly shown. Also, the species numbers (no.) are given. These numbers are also indicated in table 3. Here we mention the names which have recently changed: 130 = *Pterostichus quadripunctatus* (*angustatus*), 132 = *P. versicolor* (*coeruleascens*), 141 = *P. melanarius* (*vulgaris*), 114 = *Syntomus* (= *Metabletus*) *foveatus*, 121 = *Nothiophilus germinyi* (*hypocrita*), 99 = *Harpalus affinis* (*aeneus*), 102 = *H. solitarius* (*fuliginosus*), 104 = *H. rufipes* (*pubescens*), 106 = *H. rufipalpis* (*rufitarsis*), 73 = *Calathus rotundicollis* (*piceus*), 1 = *Abax parallelepipedus* (*ater*), 109 = *Leistus terminatus* (*rufescens*), 62 = *Bradyceillus caucasicus* (*collaris*), 65 = *B. ruficollis* (*similis*). See also: Den Boer (1977: table 2 and appendix A, part I).

species a summer breeder, and two species autumn breeders; also the preferred habitats differ highly among species (1 F, 2 H, 1 F+R, 1 F+W, 4 W, 1 A, 1 B).

If we take still closer 'genetic relationship', i.e. comparing the life-history traits of species that are taxonomically difficult to separate and thus often are considered sibling species, we detect a remarkable phenomenon: such closely related species usually occupy quite different habitats, in most cases one of the species living in (light) deciduous forest and the other(s) in open sites (heath areas or agricultural sites). For our area (Drenthe) examples of such pairs or triplets (the forest species in front) are: *Amara brunnea* / *A. bifrons*; *Amara pseudocommunis* / *A. communis* / *A. convexior*; *Agonum assimile* / *A. krynickii* (Den Boer 1962); *Agonum fuliginosum* / *A. gracile*; *Agonum moestum* / *A. versutum* / *A. viduum*; *Notiophilus palustris* / *N. germinyi*; *Nebria brevicollis* / *N. salina*; *Trichocellus placidus* / *T. cognatus*; *Bradyceillus sharpi* / *B. verbasci*; *Trechus obtusus* / *T. quadrifasciatus* (Den Boer 1965); *Pterostichus oblongopunctatus* / *P. quadrifoveolatus* (Den Boer et al. 1993); possibly also *Pterostichus strenuus* / *P. diligens*; *Harpalus quadripunctatus* / *H. laetus*; and there may be still more.

It is tempting, of course, to speculate about the possible origin of such species pairs (or triplets). It can be imagined that when man cut or burnt down more and more of the original and secondary forest of our and surrounding areas, many carabid species of the forest were deprived of their preferred habitat. Because of that most exclusively forest species, such as *Molops*, *Abax*, *Carabus*, *Cyprus* and *Calosoma*-species, may have become extinct in the course of time. Indeed, at present in the better forest remnants left in Drenthe you find only *Carabus nemoralis* and *Abax parallelepipedus*, and in dryer parts *Carabus problematicus*, but in only a very few of them possibly also *Carabus coriaceus*, *Cyprus rostratus* or *Calosoma inquisitor*.

However, the species inhabiting forest borders and openings, and light secondary forest, probably had a better chance to survive and reproduce, because during the many centuries of a primitive agriculture in these regions, many areas were abandoned because the nutrients became exhausted, and birches, rowan, poplars, and other pioneer trees would soon have grown up in them. Most of these carabid species may have had genotypes that could survive and reproduce in these abandoned agricultural fields or in the heath areas ultimately originating from these exhausted fields being used for cattle grazing. This grazing prevented recovery of the forest, and such areas gradually changed into heath and poor grassland. The latter is still indicated by incidental catches of *Pterostichus oblongopunctatus* at Kralo Heath (an old heath area) far from the nearest forest, and of *Cyprus rostratus* at

previously cultivated (buckwheat), old peat moors. In this way in the course of time large populations of such diverging genotypes may have become isolated for periods of time long enough for speciation to occur, but sufficiently short to retain a morphology about similar to that of the ancestor beetles in the forest.

Of course, we can neither confirm this hypothesis, nor repeat the historical course of events experimentally at a sufficiently large scale. Just as in all evolutionary hypotheses we can only bring up circumstantial evidence. In the present case the pair *P. oblongopunctatus* / *P. quadrifoveolatus* may give us a hint in this direction: *P. quadrifoveolatus* especially settles down at sites where woods or wood remnants have been burnt. In Den Boer et al. (1993: 243) we described a simple experiment to show that beetles of this species can easily find such sites. In the context of the above hypothesis it seems obvious that *P. quadrifoveolatus* separated from *P. oblongopunctatus* because of our distant ancestors' habit of burning secondary forest to easily clear the area for agriculture.

It may even be assumed that speciation has already occurred in response to the more recent intensification of agriculture, i.e. to the transition from a primitive agriculture over large areas to the concentration on rather small areas (in Dutch: dorps-es) that were kept fertile with cattle dung (and later with artificial fertilizer). Perhaps the pair *Calathus melanocephalus* / *C. cinctus* (Aukema 1990b) is an example of speciation as a result of such a transition; *C. melanocephalus* being more restricted to heath and other poor open soils, whereas *C. cinctus* (*erythroderus*) occurs more in abandoned agricultural fields of the present period. In accordance with this assumption *C. cinctus* lives as a kind of nomad, settling down in recently abandoned fields and disappearing again after some years, often temporarily forming mixed populations with *C. melanocephalus* (see e.g. Van Dijk 1986a). Although *C. cinctus*, like *C. melanocephalus*, is wing-dimorphic, in most sites 70% or more of its individuals are long-winged and a lot of these may fly frequently (Aukema 1990a, 1991). Populations of *C. melanocephalus* usually show less than 1% long-winged individuals (e.g. Den Boer 1977: table 3), although a newly founded population in the new IJsselmeerpolder Oost Flevoland is an exception with 20-30% long-winged beetles (Den Boer 1970; Aukema, 1990a). As could be expected for an autumn breeding nomad, *C. cinctus* produces about 75% more eggs than *C. melanocephalus* (Aukema 1991).

#### A classification of life-history patterns among carabid species

With the data presented and discussed in previous sections we tried to provisionally classify the carabid

Table 2. Provisional scheme of a classification of life-history patterns of carabid species of western Europe.

- (1) Spring breeding (summer larvae): well dispersing species with a high turnover of populations
  - a. macropterous species of unstable or temporary habitats
  - b. macropterous or wing-dimorphic species of unstable, stable or transitional and/or changing habitats
- (2) Spring breeding (summer larvae): rather badly dispersing species with a generally not very high turnover of populations and occupying stable habitats
  - a. macropterous species, possibly with low powers of dispersal
  - b. wing-dimorphic species with low powers of dispersal
  - c. brachypterous species with poor powers of dispersal
- (3) Species with a complex reproduction cycle and variable developmental periods and occupying stable habitats
- (4) Summer or autumn breeding (winter larvae): well dispersing species with a high turnover of populations
  - a. macropterous species of unstable or temporary habitats
  - b. wing-dimorphic species of unstable and/or transitional or changing habitats
- (5) Summer or autumn breeding (winter larvae): rather badly dispersing species with a not very high or low turnover of populations
  - a. macropterous species of stable and/or transitional habitats
  - b. wing-dimorphic species of stable habitats
  - c. brachypterous species of stable habitats
- (6) Late autumn breeding with summer diapause: low powers of dispersal and a low turnover of populations
- (7) Winter or early spring breeding: inhabitants of open, sandy sites with a high turnover of populations
  - a. macropterous species with good powers of dispersal
  - b. wing-dimorphic species with rather good powers of dispersal
- (8) Winter or early spring breeding: inhabitants of open, sandy sites with a not very high turnover of populations
  - a. wing-dimorphic or brachypterous species with low powers of dispersal

species of Drenthe according to some life-history traits. A scheme of this is presented in table 2.

We consider 'time of reproduction' to be the principal life-history trait, and discriminated between three groups of species: spring breeders with summer larvae, autumn breeders with winter larvae and winter breeders with summer larvae. 'Fecundity' is, as said before, partly connected with this main division: autumn breeders laying generally more and smaller eggs than spring breeders and winter breeders. However, this difference could not be incorporated in table 2, because exact data were not available for all species. A finer classification of 'fecundity' seems impractical or even irrelevant. Apart from great individual differences in egg production among females of the same population (compare table 1), egg production is determined to a great extent by quality and quantity of the food and by temperature (Van Dijk 1994). Under the highly variable conditions in the field, differences between individuals and even between most species in size of egg production may usually disappear completely. We expect that this not only applies to carabid beetles, but to arthropods in general.

More important is 'age distribution of reproduction' (semelparity versus iteroparity). But so far, we could only detect a few semelparous carabid species, most species being iteroparous (i.e. individuals do survive several winters and reproduce each year). More research has to be done on this subject.

As said before, we consider 'dispersal power' an important – though indirect – life-history trait, because it is closely connected with the turnover of populations, i.e. with the frequency of extinctions and (re)foundings

of groups in time (Den Boer 1985, 1990a, b, De Vries & Den Boer 1990). Hence, our provisional classification of life-history patterns of carabid species is based upon: 'time of reproduction', 'turnover of populations', and 'dispersal power' (expressed in terms of wing and flight-muscle development and relative frequencies of flight: catches in window traps), and 'preferred habitat(s)', in that order: table 3.

Although our classification is only based upon data of carabids from Drenthe, we expect that it will apply to large parts of West-, North- and Central Europe as well. We compared our data with those of Larsson (1939) for Denmark, Lindroth (1945: 1992) for Fennoscandia, Thiele (1977) for Western Germany, and that of several authors for Central Europe (e.g. Skuhravý 1959; Novák 1964), and we could not discover important departures from the species occurring in Drenthe.

The most striking feature of table 3 certainly is the numerical dominance of well-dispersing spring breeders of unstable and transitional habitats [groups (1)a and (1)b]. Especially among the less abundant species (table 3B) the number of *Acupalpus*, *Agonum*, *Amara*, *Bembidion* and *Dyschirius* species is remarkable. Most of these species reproduce in wet habitats, are macropterous and fly frequently. In our opinion this phenomenon highlights the impoverishment of the carabid fauna of stable habitats of our area: because of a fragmentation of natural areas, which has been pushed too far, many species with poor powers of dispersal have become extinct (Den Boer 1977; De Vries & Den Boer 1990).

The dominance of well-dispersing spring breeders

Table 3. Provisional classification of the carabid species of Drenthe (the Netherlands) according to the life-history patterns in the scheme of table 2. The numbers behind the species are used in fig. 1 and refer to Den Boer (1977: table 2 and appendix A, part I).

A. the most abundant species (mentioned in fig. 1)

- (1) a. *Agonum sexpunctatum* (18: wet), *Amara aenea* (21: agr.), *A. communis* (26: agr.), *A. famelica* (30: wet), *A. familiaris* (31: agr.), *A. plebeja* (35: agr.), *Anisodactylus binotatus* (42: agr.), *Asaphidion flavipes* (44: agr.; Coll.), *Harpalus affinis* (99: agr.), *Loricera pilicornis* (112: wet; Coll.), *Pterostichus minor* (135: wet; 95% macr.), *P. nigrithaeticus* (137: wet; see Koch & Thiele, 1980), *P. quadripunctatus* (130: burn), *P. vernalis* (140: wet)
- b. *Agonum fuliginosum* (9:wet, forest borders; 28% macr.), *Amara lunicollis* (34: wet, grass; macr.), *Bembidion lampros* (54: agr., wet; 17% macr.), *Clivina fessor* (86: agr., wet; 90% macr.), *Dyschirius globosus* (95: agr., wet; 0.1% macr.), *Notiophilus palustris* (122: forest borders; 7% macr.), *Pterostichus diligens* (133: wet, grass; 4% macr.), *P. strenuus* (139: meadows, forest; 23% macr.)
- (2) a. *Agonum assimile* (6: forest borders), *Notiophilus rufipes* (124: forest; Coll.), *Pterostichus oblongopunctatus* (138: forest), *P. versicolor* (132: heath, poor meadows)
- b. *Syntomus foveatus* (114: sandy heath; 1.2% macr.)
- c. *Agonum ericerii* (8: peat moor), *Carabus nemoralis* (78: forest), *C. arvensis* (75: heath), *Pterostichus lepidus* (134: sandy heath)\*
- (3) *Abax parallelepipedus* (1: forest; brach.), *Calathus rotundicollis* (73: light forest; 93% macr.), *Notiophilus aquaticus* (119: heathy areas; 1.2% macr.; Coll.), *N. biguttatus* (120: light forest; 74% macr.; Coll.), *Carabus cancellatus* (76: heathy areas; brach.)
- (4) a. *Harpalus rufipalpis* (106: poor grassland) *H. rufipes* (104: agr.)
- b. *Calathus fuscipes* (69: trans.; 0.9% macr.), *Pterostichus melanarius* (141: agr.; 2% macr.), *Trechus obtusus* (146: forest borders; 3% macr.)
- (5) a. *Amara brunnea* (25: light forest), *A. equestris* (29: heath), *Broscus cephalotes* (66: sand), *Harpalus latus* (103: forest, heath), *H. quadripunctatus* (105: forest borders), *H. solitarius* (102: heath), *Nebria salina* (118: trans.), *Pterostichus niger* (136: all habitats)
- b. *Agonum obscurum* (17: wet grass; 0.1% macr.), *Calathus erratus* (68: sand; 0.2% macr.), *C. melanocephalus* (70: sandy heath; 0.2% macr.), *Cymindis vaporariorum* (89: heath; 6% macr.), *Notiophilus germinyi* (121: sandy heath; 3% macr.), *Olisthopus rotundatus* (125: heath; 21% macr.)
- c. *Carabus problematicus* (80: dry forest), *Cymindis macularis* (88: sand), *Pterostichus lepidus* (134: sandy heath)\*, *Trechus secalis* (148: forest)
- (6) *Leistus rufomarginatus* (110: forest; macr.), *L. terminatus* (109: grass, trans.; macr.), *Nebria brevicollis* (117: light forest, trans.)
- (7) a. *Bradyceillus ruficollis* (65: heath), *Trichocellus cognatus* (149: heath), *T. placidus* (150: light forest)
- b. *Bradyceillus caucasicus* (62: heath), *Bradyceillus harpalinus* (64: grassy heath)
- (8) a. *Amara infima* (33: sand; 1.3% macr.), *Bembidion nigricorne* (56: sand; brach.)

\**Pterostichus lepidus* seems to be both a spring and an autumn breeder (Van Dijk, pers. comm., and Paarmann, 1990).

B. less abundant species

- (1) a. *Acupalpus brunnipes*, *A. consputus*, *A. dubius*, *A. exiguis*, *A. flavidollis*, *A. meridianus*, *A. parvulus* (dorsalis) *Agonum albipes* (ruficorne), *A. dorsalis*, *A. gracile*, *A. marginatum*, *A. muelleri*, *A. piceum*, *A. thoreyi*, *A. versutum*, *A. viduum*, *Amara anthobia*, *A. ingenua*, *A. ovata*, *A. similata*, *A. spreta*, *Bembidion assimile*, *B. bruxellense* (rupestre), *B. doris*, *B. femoratum*, *B. obliquum*, *B. pr-operans*, *B. quadrimaculatus*, *B. varium*, *Blethisa multipunctata*, *Dyschirius aeneum*, *D. luedersi*, *D. politus*, *D. thoracicus* (arenosus), *Elaphrus cupreus*, *E. riparius*, *Onthophagomimetus*, *Oodes helopiooides*, *Stenolophus mixtus*, *S. tenuon*
- b. *Amara convexior*, *Badister dilatatus*, *Bembidion guttula*, *B. tetricolum* (tustulatum), *Calosoma inquisitor*, *Chlaenius nigricornis*, *Cicindela campestris*, *C. hybrida*, *Demetrias atricapillus*, *Dromius agilis*, *D. angustus*, *D. melanocephalus*, *D. quadrimaculatus*, *D. spilotus* (quadrimaculatus), *Harpalus anxius*, *Notiophilus substristriatus*, *Panagaeus cruxmajor*
- (2) a. *Agonum krynickii*, *A. livens*, *A. moestum*, *Anisodactylus nemorivagus*, *Badister bullatus* (bipustulatus), *B. sodalis*, *B. unipustulatus*, *Bembidion humerale*, *Lebia chlorocephala*, *Odoacantha melanura*
- b. *Carabus clathratus*, *C. granulatus*, *Syntomus (Metabletus) truncatellus*, *Pterostichus antracrinus*
- c. *Bembidion mannerheimi* (unicolor), *Carabus nitens*, *Cicindela germanica*, *Cyphus caraboides rostratus*
- (3) *Carabus coriaceus*
- (4) a. *Amara apricaria*, *A. aulica*, *A. bifrons*, *A. consularis*, *A. convexiuscula*, *A. fulva*, *A. majuscula*, *Asaphidion pallipes*, *Calathus ochropterus* (mollis), *Harpalus distinguendus*, *H. rubripes*, *H. smaragdinus*, *H. tardus*, *Trechus quadrifasciatus*, *T. discus*
- b. *Calathus cinctus* (erythroderus)
- (5) a. *Amara pseudocommuni*, *A. kulti*, *A. praeternissa*, *A. quenseli*, *Miscodera arctica*, *Nebria livida*
- b. *Calathus ambiguus*, *Synuchus nivalis*
- c. *Calathus micropterus*, *Masoreus wetterhalli*, *Patrobus atrorufus* (excavatus), *Stomis pumicatus*
- (6) *Leistus spinibarbis*
- (7) a. *Bradyceillus verbasci*
- b. *Bradyceillus cskii*
- (8) a. *Bradyceillus sharpi*

3A: between brackets behind the species an indication of the preferred habitat.

macr.= macropterous; brach.= brachypterous; agr.= occupying agricultural fields and other ruderal or disturbed sites; wet= occupying banks of pools and rivers and other wet sites; burn= reproduces at sites where woods or remnants of wood has been burnt; grass= prefers dense grass vegetations; trans.= occupying transitional sites between forest and heath or grassy vegetations; sand= occupying blown sand areas with only little vegetation; Coll.= specialized in the hunting of Collemboles.

For estimates of dispersal power and turnover frequencies of the most abundant carabid species of Drenthe see Den Boer (1990a: table 1; 1990b: table 4).

3B: between brackets behind the species old names.

over less well-dispersing ones is less apparent among the most abundant species (table 3A), because the number of wet habitats has also decreased dramatically in the last hundred years. Only a few of the species of wet habitats could still be called 'abundant'. But the difference between the number of well-dispersing [(1)a+(1)b] species (A: 21; B: 57) and that of the badly dispersing [(2)a+(2)b+(2)c+(3)] species (A: 14; B: 18) is not significant ( $\chi^2 = 2.95$ ;  $P = 0.10$ ). As autumn breeders are almost restricted to dryer habitats the difference between the numbers of well-dispersing spring and autumn breeders is about the same for abundant and less abundant species ( $\chi^2 = 0.078$ ;  $P = 0.80$ ), and a similar result is found for the badly dispersing species ( $\chi^2 = 1.80$ ;  $P = 0.20$ ). Hence the abundant species (table 3A) are a fair sample of the carabid species of Drenthe.

Both for the spring breeders and for the autumn breeders the different life-history patterns we distinguish more or less reflect the expected evolutionary processes. When in the course of vegetational succession many previously unstable habitats become more and more stable, well-dispersing species occupying these habitats will gradually lose their powers of dispersal (Den Boer 1977, 1990a). As there are always unstable habitats, however (banks and moors, new openings in the forest resulting from storm or fire) most well-dispersing species will survive. Some of these will settle also in localities where stable habitats are not destroyed on a large scale by reclamations for agriculture and urbanisation. Today in the Netherlands there is a growing tendency to make 'new nature', e.g. by returning agricultural fields and the water meadows along our great rivers into more natural areas. Especially when these areas of 'new nature' become sufficiently large we may expect that ultimately among the (carabid) species that occupy these new areas the evolution from well dispersing to less well dispersing ones will be stimulated again.

## DISCUSSION

'Life history theory deals directly with natural selection, fitness, adaptation, and constraint. It contributes to evolutionary thought the analysis of the phenotypic causes of variation in fitness and exposes the pervasive tension between adaptation and constraint, brought here into especially sharp contrast by the simultaneous application of optimality theory, quantitative genetics, trade-offs, and the comparative method to the explanations of the same patterns.' (Stearns 1992: 9).

This sentence indicates clearly that life-history theory in the first place indeed is theory (see also Roff 1992), because 'natural selection' is difficult to study directly under natural conditions, whereas both 'fit-

ness' and 'adaptation' are difficult to objectify and quantify. Therefore, life-history theory is mainly based on thoughts about natural selection, fitness, adaptation and constraint, and these thoughts are illustrated by mathematical models and some general experience with special groups of organisms (vertebrates?). This does not mean, however, that occupation with life-history theory is a waste of time. On the contrary, contemplating such subjects is necessary to come to an efficient collecting of adequate data. But meanwhile life-history theory is also highly subject to changing fashion, and therefore is still largely based upon presently fashionable ideas about competition, optimisation and restricted energy-budgets.

'In life history evolution the patterns to be explained are the full diversity of life cycles in living things. These range from the familiar cycle of birth, reproduction and death in birds and mammals, through alternating sexual and asexual generations of cladocerans, rotifers and some beetles and the modular life histories of many plants and bryozoans, to complex life cycles of algae, parasites, and corals. In what framework can all life histories be understood as variations of a few general themes?' (Stearns 1992: 11).

Hence, the task of life history theory should be, according to Stearns, to find a few 'general rules' with which life histories can be classified in groups. In our opinion, it is best to start this exercise with field data, as we have tried to do in table 3.

As 'habitats' are defined and classified differently for the different groups of organisms Stearns (1992) thinks it both simpler and more general to leave 'habitats' out of the classifications of life histories.

'Nevertheless, well qualified opinions assert it is worth trying to relate habitat to life history (...). These authors want to explain patterns relating certain lineages to certain habitats. To satisfy, such explanations should demonstrate a mechanism that links habitats to life histories. According to this book, one candidate is the impact of habitats on age- and size-specific fecundity and mortality schedules. Thus we seek to understand not habitat ----> life history but habitat ---> mortality regime ---> life history.' (Stearns l.c.: 208).

We are sure that 'habitat' has more to contribute to life-histories than 'mortality regimes'. For instance, both 'fecundity', 'time of reproduction' and 'time of first reproduction' may be importantly influenced by 'habitat', more so in poikilothermic animals than in homioiothermic ones. In carabid beetles egg production is not only determined by genetic characters, basal metabolism (table 1) and food, but also to a high degree by temperature (Van Dijk 1983; Aukema 1991); both food quality and quantity and temperature are highly affected by 'habitat'. We have shown

how spring and autumn breeding are connected with 'habitat' and season (climate). Therefore, to adequately recognize life-history patterns it does not suffice to consider 'habitat' as the determinant of 'mortality regimes'.

Another common belief is the assumption of the universal occurrence of trade-off's:

'One example is the production of spines and elongate helmets in waterfleas, *Daphnia*, in response to dissolved molecules that indicate the presence of invertebrate predators that prey less effectively on spiny, helmeted *Daphnia*. Helmets and spines are costly, individuals that do not produce them have higher reproductive rates, and therefore when predators are not present, the spines and helmets are not produced. This definition is most appropriately applied to variation within populations.' (Stearns 1992: 16).

But such an application is not adequate in all kinds of populations. As mentioned before, Aukema (1991) showed that long-winged morphs of *Calathus cinctus* and *C. melanocephalus* produce more eggs than short-winged ones, in spite of the fact that the production of functional wings and wing-muscles must be 'costly'. Moreover, Aukema mentions other examples of beetles where the winged morph is more productive than the wingless morph. 'From the data on fecundity of short-winged and long-winged *C. cinctus* and *C. melanocephalus* presented here, it is evident that in both species it is not the brachypterous morph but the macropterous one that has a higher Darwinian fitness.' (l.c.: 125). This also means that the gradual reduction of dispersal power in wing-dimorphic carabid populations living in stable habitats is not caused by a higher fitness of the brachypterous morphs, expressed in a higher egg production, as was supposed by e.g. Darlington (1943), and still stated by Roff (1990, 1994), but by winged individuals flying away from the population area, though often these do not succeed in colonizing new sites.

'According to Williams (1966) ..., an adaptation is a change in a phenotype that occurs in response to a specific environmental signal and has a clear relationship to that signal that results in an improvement in growth, survival, or reproduction.' (Stearns 1992: 16).

If we apply this definition of adaptation to dispersal power, we may establish that a decrease or increase of dispersal power is a change in the frequency of genotypes that occurs in response to the environment becoming more stable or unstable. And, as we saw above (Aukema 1991), this may show a clear relationship either to survival – decrease of dispersal power in a stable habitat – or with reproduction – increase of dispersal power in an unstable habitat. Nevertheless, we do not expect that Stearns did have had dispersal power in mind as an example of a functional adapta-

tion, because at first sight flying away from the population area where survival and reproduction are still possible, for many individuals only seems to mean suicide. However, since the survival time of each local population is limited, without any dispersal and the connected chance to colonize other suitable sites, the species will not survive much longer than the longest-living local population. In our opinion, this contradiction between individual profit and profit for the species has prevented evolutionary biologists seeing the evolutionary and ecological significance of dispersal and dispersal power.

Summarizing, this provisional comparison of life-history patterns of carabid species in relation to environmental conditions does not give much support to the current theoretical constructions and models of evolutionary biologists as expounded by Williams (1966), criticized by Stearns (1976), and extensively discussed by Stearns (1992) and Roff (1992). Most probably this lack of correspondence between theory and field practice results from the fact that even related animal species adapt to their habitats from very different starting-points. Because of that, the 'solutions' created by natural selection are also very different. Many of these 'solutions' may be far from 'optimal', simply because the historically given starting-points did not allow better ones.

Therefore, before continuing the construction of theoretical models of the evolution of life histories it seems necessary, or at least useful, to do more comparative investigations on life-history patterns of species other than carabids.

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